CONTRASTING FEEDING STRATEGIES IN BIVALVES FROM THE SILURIAN OF GOTLAND

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ABSTRACT. Two examples of contrasting feeding strategies in bivalves from the Silurian of Gotland are presented. The first shows a deposit-feeding community of protobranchs in which non-siphonate species greatly dominate siphonate ones. This is probably the result of extensive bioturbation by the non-siphonate species causing agitation of the fine-grained sediment and consequent disturbance of the feeding of siphonate species. Tiering of this community is also suggested, based on observations on abundant, silicified material. The second example depicts shallow subtidal life associations of *Ilionia prisca* in preferred orientation. This species shows special characteristics typical of extant deeply burrowing suspension-feeders of the superfamily Lucinacea. It is suggested that *Ilionia prisca* had a unique feeding strategy of anterior inhalation through a mucus tube, and also that it oriented itself obliquely to the direction of wave action, both for optimal intake of suspended food particles and for the avoidance of inhaling its own waste products. Possibly *Ilionia prisca* also lived in symbiosis with sulphur-oxidizing bacteria. The beds discussed are intercalated with shales and it is assumed that the whole bivalve population was instantaneously killed off when smothered by mud.

BIVALVES are perhaps the most thoroughly investigated of all marine invertebrates and many studies have been devoted to the feeding habits of this group. Throughout their evolutionary history, bivalves have occupied a large spectrum of aquatic habitats and are thus well suited for palaeoecological reconstructions.

The feeding habits and trophic relations of benthic invertebrates have been classified by various workers in different ways (e.g. Stanley 1968; Walker and Bambach 1971). Most bivalves are generally considered to be suspension feeders or deposit feeders or carnivores. The classification of organisms as true suspension feeders or true deposit feeders, however, is made difficult by the presence of 'opportunistic feeders', i.e. those capable of using more than one feeding method (Cadée 1984).

Deposit feeders ingest organic matter trapped in the substrate in which they live and therefore must actively move about in search of food. Their gills are simply built and mainly used for respiration, while the collection of food particles is provided by palp proboscides. Siphons, when present, are used for respiration (Cox 1969).

The protobranchs discussed in this paper include one opportunistic deposit feeder, the solemyoid *Janeia silurica* (believed to have been symbiotic with chemoautotrophic bacteria: see Liljedahl 1984a, 1984b, 1984c).

In suspension feeders, the gills are more complex than those of the deposit feeders and are mainly used for food collection. Suspension feeders normally remain fixed in one position and passively feed on particles which come to them through the water. When present, siphons are, in contrast with the deposit feeders, used for feeding. Also within the suspension feeders 'opportunistic' feeders are present. The Silurian *Ilionia prisca* is assumed to have lived in symbiosis with chemoautrophic bacteria and is thus considered an 'opportunistic' filter feeder (Liljedahl in prep.).

Bivalves play an important role in the tiering relationships (relative vertical (ecological) positions of organisms within a community) in many Recent biotas, where different trophic categories or feeding groups may be recognized (Ausich and Bottjer 1984).

The chemical stratification and related environmental changes within a sediment may be

considerable. Accordingly, the ecological relationships of organisms downwards from the surface can be more extreme below the sediment/water interface than above it.

The first example considered in the present paper, is represented by deposit feeders. In this, community tiering may be established (for detailed analysis see Liljedahl 1985). Indirect competitive interactions may also have been present here: the feeding habits of one trophic group (the non-siphonate deposit feeders) is suggested to have made the substrate unsuitable for representatives of another trophic group, the siphonate deposit feeders (see Rhoads and Young 1970; Levinton and Bambach 1975).

As filterers, suspension feeders are sensitive to sudden environmental changes (in contrast to deposit feeders). Above the sediment/water interface, ecological stratification may also occur, depending on different susceptibility to fouling among the suspension feeders.

The second example is provided by the deeply buried 'opportunistic' suspension feeder *Ilionia prisca* (Hisinger). It inhabited a substrate of low species diversity in a shallow subtidal environment of low oxygen and high sulphur content, unsuitable for most other bivalves. It is suggested that *Ilionia prisca* oriented itself with its anterior-posterior axis obliquely to wave movement, i.e. with its anterior inhalant mucus tube against the flow of suspended food particles. By analogy with its living relatives (Reid and Brand 1986) it is also assumed that *Ilionia prisca* housed chemoautotrophic bacteria in the gills, the bacteria being important nutritional providers for the bivalve (Liljedahl in prep.).

## INTERACTIONS BETWEEN THE DEPOSIT-FEEDING BIVALVES OF MÖLLBOS

The material from Möllbos 1 consists of 2743 silicified valves, of which 684 are articulated. Only one specimen (*Nuculodonta gotlandica*) has been observed in life-position (Text-fig. 1G). They were all isolated by acid etching and the preferred life-positions of each of the Möllbos species are thus mainly based on morphological and statistical grounds by analogy with modern counterparts.

One of the advantages of the acid etching method is that the whole preserved shelly fauna is recovered, i.e. all sizes are represented (Liljedahl 1984*a*). Above all it is possible to obtain enough material for fairly reliable statistical processing (Liljedahl 1985).

The bivalves form an important constituent of the Möllbos fauna. Although it is a typical soft-bottom community, this fauna contains a conspicuous amount of sessile benthos such as stromatoporoids, tabulate corals, rugose corals, crinoids, etc. probably due to close vicinity to a reef. It abounds in infaunal burrowers, e.g. protobranch bivalves, gastropods, and annelid worms (Liljedahl 1983).

The Wenlockian Halla Beds at Möllbos consists of a compact, strongly argillaceous calcilutite which is fairly hard due to silification (Liljedahl 1983, p. 8). The high percentage of deposit feeding

TEXT-FIG. 1. A, *Nuculoidea lens*. External dorsal view of articulated specimen, anterior to the left, SGU TYPES 894, 895, sample G77-28LJ, ×4·3. B, *Nuculodonta gotlandica*. External dorsal view of articulated specimen, anterior to the left, SGU TYPES 1202, 1203, sample G79-82LJ, ×3·9. C, *Nuculoidea lens*. External lateral view of a left valve, SGU TYPE 901, sample G77-28LJ, ×3·9. D, *Nuculodonta gotlandica*. External lateral view of a left valve, SGU TYPE 1036, sample G78-2LL, ×4·4. E, *Nuculoidea lens*. Internal postero-ventral view of holotype (right valve) showing from left to right, anterior adductor muscle scar, anterior pedal protractor muscle scar (first arrow from the left), visceral attachment muscle scar (second arrow), anterior pedal retractor muscle scar (third arrow), and pedal elevator muscle scar (fourth arrow), SGU TYPE 842, sample G77-28LJ, ×3·5. F, *Nuculodonta gotlandica*. Internal posteroventral view of a right valve showing from left to right, anterior adductor muscle scar, anterior pedal protractor muscle scar (first arrow from the left), anterior pedal retractor muscle scar (second arrow), and visceral attachment muscle scar (third arrow), SGU TYPE 1200, sample G79-82LJ, ×4. G, *Nuculodonta gotlandica*. Only specimen of the bivalve fauna of Möllbos 1 found in life-position, just below original sediment surface, LO 6084t, loose boulder, ×1·3. All specimens are silicified and all samples are from Möllbos 1.
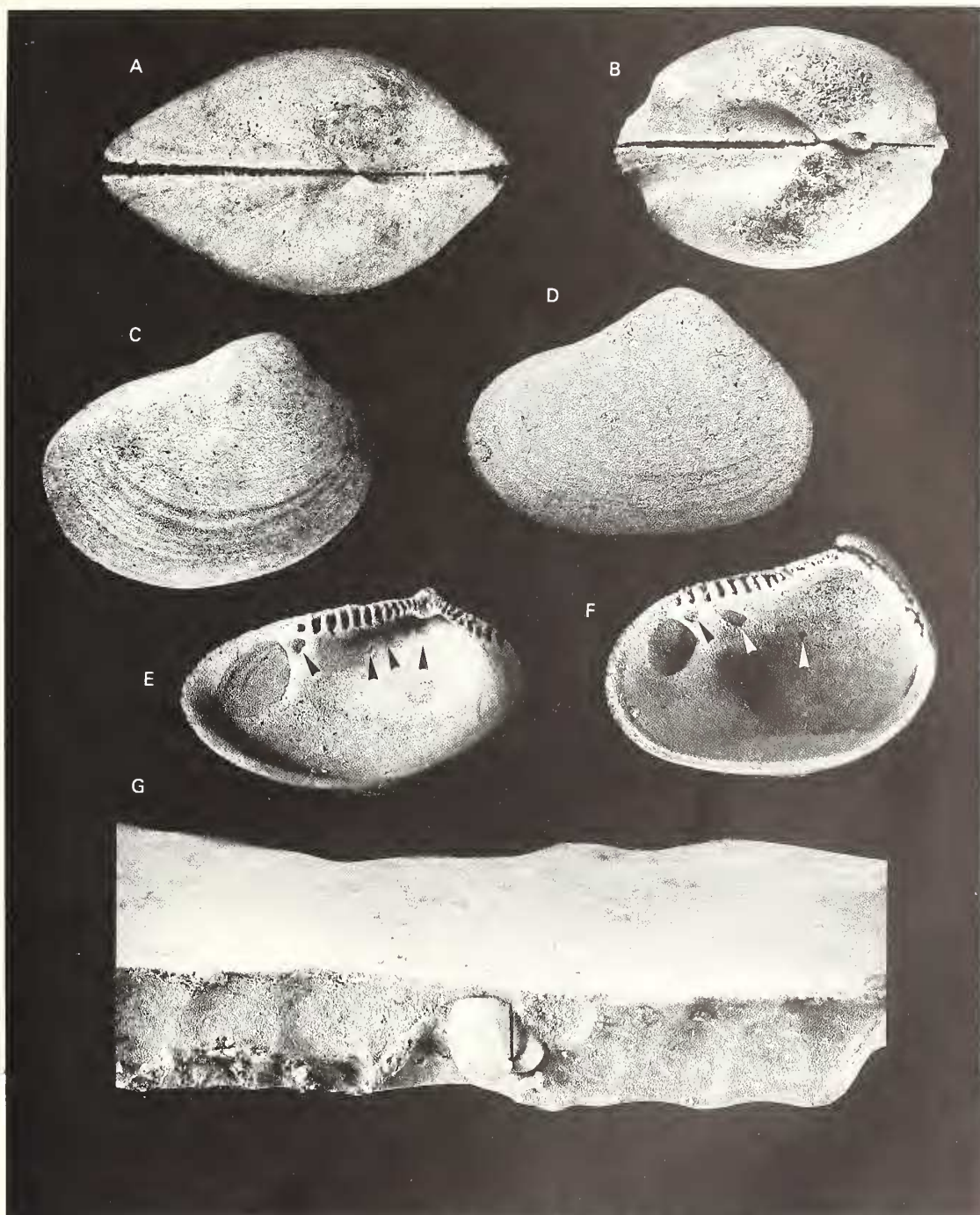
TEXT-FIG. 1. For legend see opposite.

animals suggests that this sediment was rich in bacteria, as is often the case in fine grained substrates (Zobell 1938: Newell 1970).

It is concluded that the Möllbos infaunal bivalve fauna is autochthonous and undisturbed except for *post mortem* phenomena, such as disturbances by scavengers and burrowing deposit feeders (Liljedahl 1985; also see Johnson 1960 for criteria for life associations).

The bivalve fauna is numerically dominated by deposit feeding species (90% of the bivalve population: Liljedahl 1985). It comprises four nuculoid species, *Nuculodonta gotlandica* Liljedahl, 1983 (44% of Möllbos bivalves), *Nuculoidea lens* Liljedahl, 1984 (27%), *Palaeostraba baltica* Liljedahl, 1984 (0·7%), *Caesariella lindensis* (Soot-Ryen, 1964) (0·4%), and one solemyoid, *Janeia silurica* Liljedahl, 1984 (18%).

Shell morphology of the different deposit feeding bivalves shows a common theme with minor variations (Liljedahl 1984*a*). The impressions of pedal and other accessory muscles are evident (Text-fig. 1E, F) and the anterior part of the shell is large, indicating a strong and functional burrowing foot (see reconstructions in Text-fig. 3). Also the adductor muscle scars are generally deep, suggesting powerful closing, and thus efficient removal of debris and other indigestible material from the mantle cavity. Much of the space of the mantle cavity was probably occupied by the foot and its muscles, whereas the gills most probably were moderate in size (note the opposite relation in stationary suspension-feeding species).

Shell morphology indicates, in combination with statistical data, a probable life position in the substrate as shown in Text-figure 3. *Nuculodonta gotlandica* has a thick, robust shell, deep adductor muscle scars, prominent pedal muscles scars, and lacks any indication of siphons (Text-fig. 1B, D, F, G). Its shell shape suggests a moderately slow rate of burrowing (Liljedahl 1984*a*, fig. 4). Accordingly, it is proposed that it lived close to the sediment/water interface (Text-fig. 3).

Nuculoidea lens has a somewhat thinner shell, deep adductor muscle scars, clear pedal muscle scars and no indication of siphons (Text-fig. 1A, C, E). The shell shape suggests a moderately slow rate of burrowing (Liljedahl 1984*a*, fig. 4). Most probably it lived somewhat deeper in the substrate than *Nuculodonta gotlandica* (Text-fig. 3; conclusion partly based on articulated valves relative to disarticulated valves; see next section).

Janeia silurica has a thin, elongate and compressed shell and deep adductor muscle scars (Text-fig. 2E–G), all features typical of a rapidly burrowing bivalve (see Liljedahl 1984*a*, fig. 4, 1984*b*). Although fragmented (due to its thin shell), a considerable number of specimens are articulated (31%). Furthermore, the configuration of the muscular impressions suggests that it may have lived symbiotically with chemo-autotrophic bacteria at a sulphide-rich level of the bottom (see Cavanaugh *et al.* 1981) where it did not have to compete for food with other species (Liljedahl 1984*b*). Thus, it seems that of all bivalves of this community *Janeia silurica* inhabited the deepest level (Text-fig. 3).

All three species have an anteriorly expanded shell and a well developed system of pedal muscle scars, just as in extant forms capable of active burrowing.

Palaeostraba baltica has a thin shell with a shape suggesting rapid burrowing (Text-fig. 2B, D; Liljedahl 1984*a*, fig. 4). It also has a posterior sulcus indicating the presence of siphons. Both characters suggest that it lived at a position somewhat below the sediment surface (Text-fig. 3).

Caesariella lindensis has a thin shell and a shallow pallial sinus containing siphonal retraction muscle scars, which indicates the presence of siphons. Its shell form suggests slow burrowing (Text-fig. 2A, C: Liljedahl 1984*a*, fig. 4) and its life position is thought to have been just below the sediment surface (Text-fig. 3).

The two last mentioned species have conspicuous, but not especially deep, scars of pedal muscles suggesting fairly good burrowing ability.
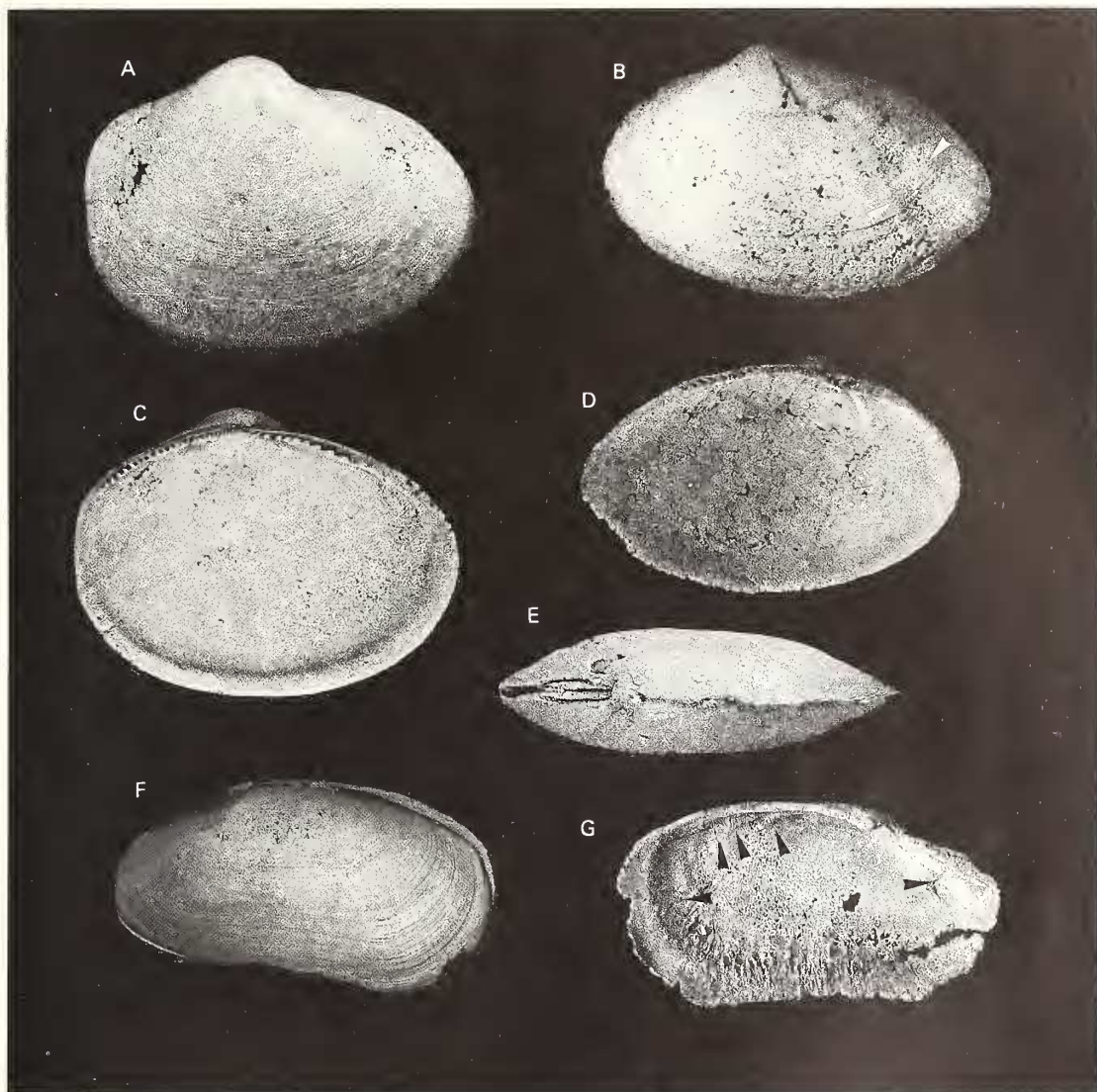
TEXT-FIG. 2. A, *Caesariella lindensis*. External lateral view of right valve specimen of holotype, SGU TYPE 3606, sample G79-78LJ, × 3·4. B, *Palaeostraba baltica*. External lateral view of holotype (left valve), note posterior sulcus (at arrows), SGU TYPE 3498, sample G78-2LL, × 4·3. C, *Caesariella lindensis*. Internal lateral view of left valve specimen of holotype, SGU TYPE 3607, sample G79-78LJ, × 3·4. D, *Palaeostraba baltica*. Internal lateral view of holotype, × 4. E–G, *Janeia silurica*; E, external dorsal view of articulated specimen, anterior to the right, SGU TYPES 3426, 3427, sample G77-29LJ, × 1·8; F, external lateral view of articulated specimen, anterior to the right, same specimen as E, × 1·7; G, internal lateral view of right valve specimen of holotype, SGU TYPE 3608, sample G79-79LJ, × 2·4. All specimens are silicified and all samples are from Möllbos 1.

TIERING OF THE MÖLLBOS BIVALVE COMMUNITY

Nuculodonta gotlandica makes up 50·0% of the counted 2743 protobranch valves (protobranch shell debris estimated as double that amount), *Nuculoidea lens* 28·7%, *Janeia silurica* 19·9%, *Palaeostraba baltica* 0·9%, and *Caesariella lindensis* 0·4%.
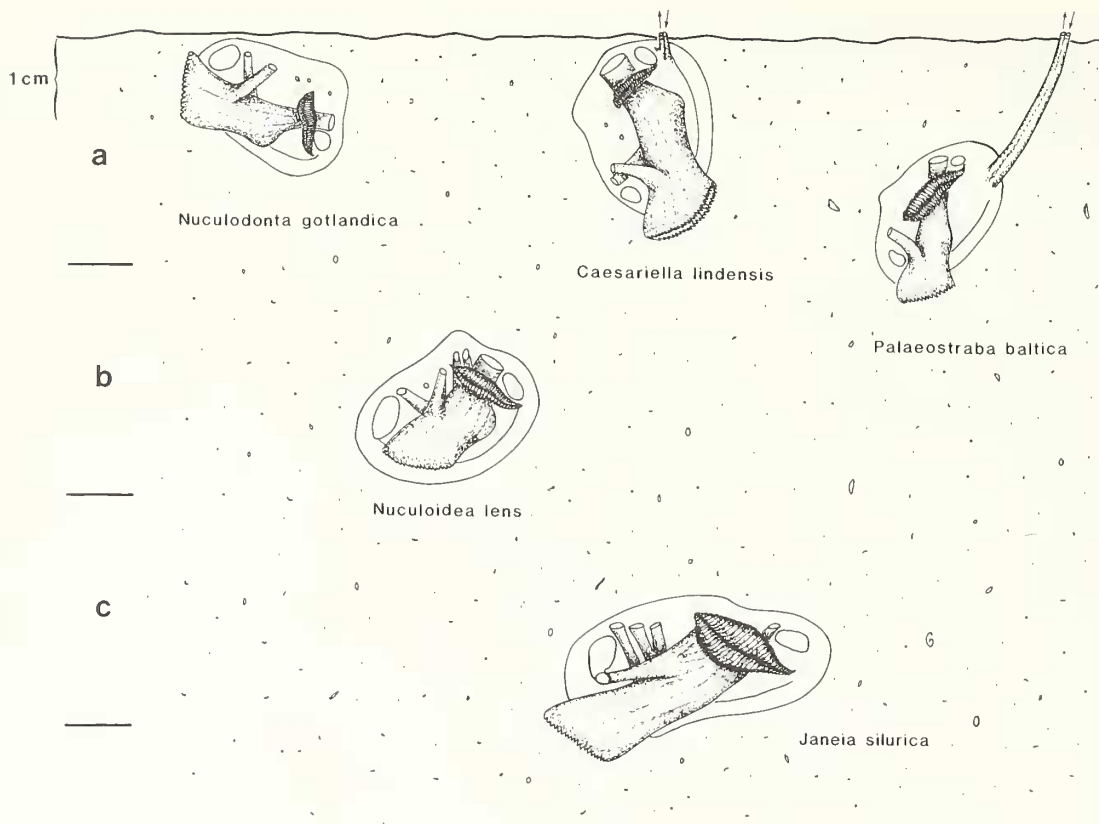
TEXT-FIG. 3. Suggested life-position and reconstructions of the foot and gills of the protobranchs of Möllbos. Arrows indicate in- and exhalant currents, respectively. a, b, and c represent different tiers. Maximum depth approx. 7 cm. Sizes relative to each other.

Seventeen samples were taken from seventeen beds in three vertical sections about ten metres apart. Due to faulting, however, these can not be correlated (Liljedahl 1984*a*, p. 82). The species ranking is shown in Text-figure 4.

Nuculodonta gotlandica is ranked first in sixteen samples and second in one. *Nuculoidea lens* is ranked first in one sample, second in twelve, and third in four. *Janeia silurica* is ranked second in five samples and third in twelve. *Palaeostraba baltica* is ranked fourth in eleven samples and fifth in one. *Caesariella lindensis* is ranked fourth in three samples and fifth in three.

The rates of occurrence of the three most abundant species suggest co-existence at different tiers. Seven samples contain *N. lens* and *J. silurica* in fairly equal numbers and in all the remaining samples but one (G79–3), the difference in occurrence is about 14%. This strengthens the assumption that the various species co-existed but at different tiers with *J. silurica* being the deepest, in a similar manner to the *Nucula proxima – Solemya velum* relationship. In the latter *Nucula proxima* is attracted to the burrow openings of *Solemya velum*, representing a positive association (Levinton 1977, p. 208, fig. 13).

N. lens and *J. silurica* also show a significantly higher rate of articulated valves (33·8 % and 31·0%, respectively) than *N. gotlandica* (17·9 %), indicating a deeper life-position of the two first mentioned. The higher rate of articulated valves of *N. lens*, suggested to have lived at a shallower depth than *J. silurica* and accordingly exposed to more bioturbation, may be explained by its taxodont dentition resisting shearing stresses better than the edentulous hinge of *J. silurica*.
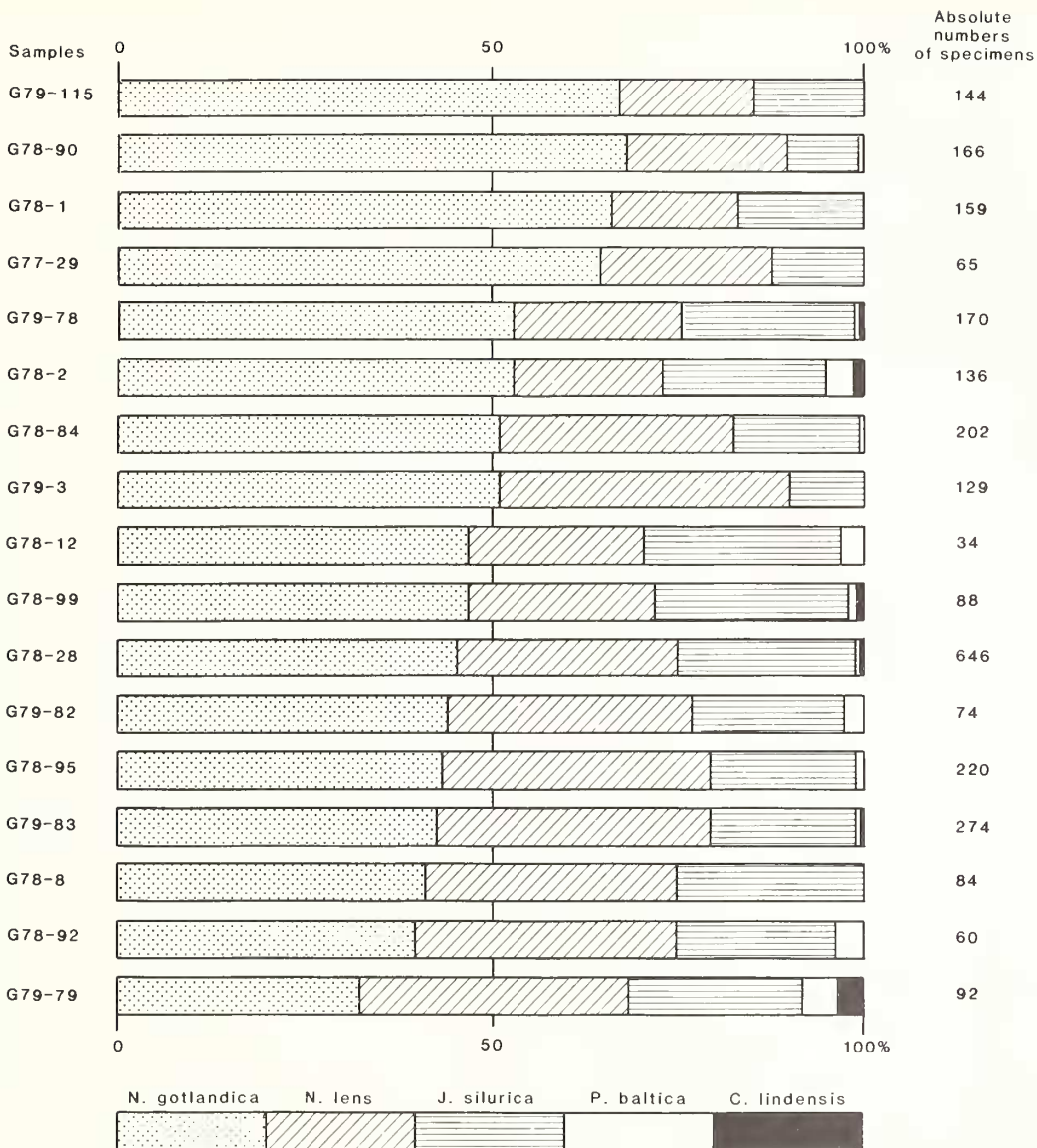
TEXT-FIG. 4. Percentage frequencies of the protobranchs of Möllbos.

The siphonates *Palaeostraba baltica* and *C. lindensis* are greatly outnumbered and together make at most 7·6 % of the deposit feeders of this bivalve community. *P. baltica* occurs in twelve samples while *C. lindensis* appears in six. In six of the eight samples in which *N. gotlandica* dominates over *N. lens* and *J. silurica* taken together, *P. baltica* and *C. lindensis* are absent. On the other hand, in eight of the nine samples where *N. lens* and *J. silurica* together dominate *N. gotlandica*, either *P. baltica* or *C. lindensis* or both are present. Thus, *P. baltica* and *C. lindensis* appear to have co-existed with *N. lens* and *J. silurica* and probably inhabited feeding levels different from them, i.e. they occupied the shallowest level, in which *C. lindensis* lived just beneath the sediment/water interface.

Thus when *N. gotlandica* was abundant, the two siphonate deposit feeders were totally crowded out, or almost so. Their feeding activity was probably disturbed by the intense bioturbation of *N. gotlandica* near the sediment surface.

MODE OF LIFE OF *ILIONIA PRISCA* FROM GROGARNSHUVUD

The material from Grogarnshuvud 1, which constitutes the second example, consists of field observations of 151 *in situ* specimens from three separate beds and additional specimens from other beds. All specimens are preserved in calcium carbonate.

Evolutionary aspects

The Lucinacea, constituting an ecologic group of infaunal mucus feeders, hold a unique position in bivalve evolution in being the first known suspension feeders to inhabit a deep life position. They seem to be unrelated to 'normal' siphonate suspension feeders from which they differ through their unusual posterior siphon, their unique anterior inhalant mucus tube, and their anterior-to-posterior flow of water through the mantle cavity (Allen 1958), and in living in symbiosis with bacteria (Dando *et al.* 1986; Reid and Brand 1986).

The earliest representatives of Lucinacea appeared in the Silurian, much earlier than the first appearance of more typical siphonate infaunal bivalves of the Carboniferous. True siphonate suspension feeders, virtually absent in the Palaeozoic, underwent their extensive radiation first in the Mesozoic era (McAlester 1966; Stanley 1968).

Functional morphology

A number of characters of extant Lucinacea are unique among bivalves and some of them may be recognized in *Ilionia prisca* [Hisinger, 1837; original combination *Tellina (Lucina?) prisca*] as well (Text-figs 5 and 6).

One of the most striking external features is the posterior sulcus (Text-fig. 5c) which in Recent species normally indicates the presence of siphons and also follows the line of attachment of the gills (Allen 1958, p. 427; cf. muscle scars in corresponding position of *Ilionia prisca* in Text-fig. 5B).

Another characteristic is the hypertrophied, linguiform anterior adductor muscle (often conspicuously contrasting in specimens of *Ilionia prisca*, see Text-fig. 5A, B), the surface epithelium of which is ciliated and which sorts the food particles entering by the anterior inhalant tube.

A third characteristic of the Lucinacea is the channel (passage area in *Ilionia prisca*, Text-figs 5B and 6) between the anterior adductor muscle and the pallial attachment of the mantle (pallial line) in which the vermiform part of the foot can operate (Allen 1958, p. 435).

The foot of Lucinacea is highly specialized and in some species it can extend to more than ten times the length of the shell. The mucus inhalant tube is constructed in the sediment by the anterior, vermiform part of the foot. In some species the posterior part of the foot or heel may be protruded and burrowing performed (Allen 1958, p. 448).

Recent lucinaceans lack a posterior inhalant siphon. Instead they have evolved the ability to form an anterior inhalant mucus tube in the sediment. The posteriorly situated exhalant siphon, if present, is unique since no siphonal retractor muscles of normal type (cf. Stanley 1968), are present and therefore no pallial line is formed in the shell (Allen 1958, p. 430).

In soft part morphology the Lucinacea are characterized by a thickened ctenidium consisting of single demibranchs, gill-mantle fusion, the existence of mantle gills and a type V stomach (Purcheon 1958). Finally, representatives of the two families Lucinidae and Thysiridae live in symbiosis with sulphur-oxidizing bacteria (Reid and Brand 1986).

Compared to extant Lucinacea the shell of *Ilionia prisca* is more elongate in antero-posterior direction, due to its extremely elongate anterior adductor muscle. This could also indicate that *Ilionia prisca* was better suited for rapid burrowing. The impressions of the anterior adductor muscle scar are larger and consequently the contractile power of this muscle is likely to have been considerably greater. The conspicuously expanded anterior adductor muscle scar also must have
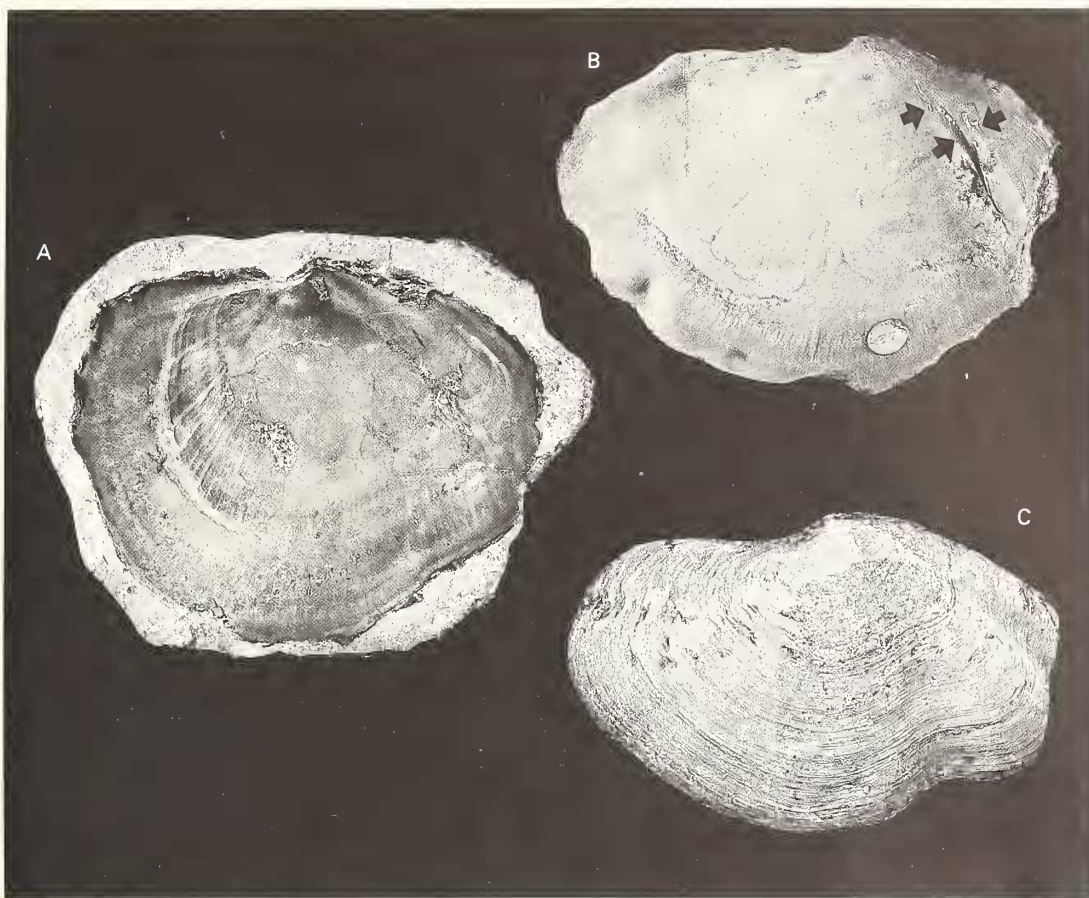
TEXT-FIG. 5. *Ilionia prisca.* A, internal view of a single right valve, note conspicuous anterior adductor muscle scar, RMMO 17790, Östergarn, Ludlovian Hemse Beds, × 1·2. B, lateral view of internal mould of articulated specimen, anterior to the left, note gill attachment muscle scars (arrowed) and radial muscle scars of the mantle edge, note also space between the anterior adductor muscle scar and pallial line, RMMO 149879, Östergarn, Ludlovian Hemse Beds, × 1·2. C, external lateral view of a single left valve, RMMO 158171, Histilles, Ludlovian Hemse Beds, × 1.0.

reduced the space available for the gills, which were comparatively smaller than those of its living relatives. This could have resulted in a less efficient sorting ability of the gills as compared to its Recent relatives.

On the other hand, if the greatly extended ventral part of the anterior adductor muscle (the muscle scar being considerably larger than in modern lucinaceans) acted as a sorting area for inhaled particles, this could have compensated for smaller sized gills.

Ilionia prisca is integripalliate, as are Recent lucinaceans, but is believed to have had a posterior exhalant siphon, as indicated by the conspicuous external posterior diagonal sulcus (cf. Allen 1958, p. 449).

In some specimens the ventral margin is undulating. This feature, also present in for example *Grammysia*, in combination with the elongate shell form may have helped in rapid downward burrowing (see Bambach 1971; Marsh 1984).

The Silurian *Ilionia prisca* shows such remarkable conformity with living Lucinacea that it may

safely be assumed that *Ilionia prisca* had adopted the unusual lucinacean life habit (see McAlester 1965), a mode of life already initiated in Ordovician times by the genus *Babinka*. In addition to the suspension feeding habit, *Ilionia prisca* possibly also housed sulphur-oxidizing bacteria in its gills, in analogy with its living relatives (cf. Reid and Brand 1986).

Life habit

Extant Lucinacea are uniquely adapted for deeply burrowing suspension-feeding in environments with a low oxygen and a high sulphur content (Southward 1986). In their gills they have chemoautotrophic endosymbiotic bacteria (sulphur-oxidizing) which act as important nutritional providers for the bivalve (Berg and Alatolo 1984; Spiro *et al.* 1986). Some authors consider this symbiosis to be the main feeding mode (Reid and Brand 1986).

Besides the bacterial symbiosis the lucinaceans feed in the following way (Text-fig. 6A). In a deeply buried position, nutrient-laden water is drawn into the mantle cavity through an anterior mucus-lined tube in the sediment, made by the vermiform part of the foot. The water passes the ciliated ventral part of the anterior adductor muscle which acts as a sorting area before the water reaches the gills. The exhalant water with indigestible particles is expelled posteriorly by rapid contraction of the adductor muscles, in some species through a posterior siphon to the sediment surface, in others directly into the sediment (Allen 1958).

Based on comparative anatomy with its Recent descendants (Allen 1958), it is concluded that *Ilionia prisca* was a deeply burrowing, shallow subtidal suspension feeder (Text-fig. 6B). *Ilionia prisca* lived in a soft, carbonate mud of low oxygen and high sulphur content, bioturbated to the extent that the original lamination is completely lost (Sundquist 1982, p. 87). In equivalent sediments today the diversity of suspension-feeding bivalves is commonly low (Buchanan 1958; Rhoads 1970; Rhoads and Yonge 1970). Indeed, species diversity is low at Grogarnshuvud 1 (see Sundquist 1982, p. 88), including only three additional bivalve species, an undescribed, epi-byssate suspension feeder, a protobranch nuculoid and the protobranch solemyoid *Janeia silurica*. The suspension feeder (found as disarticulated valves only) was most probably exotic and transported into the present bivalve community together with empty orthocone nautiloid shells during ephemeral events (see Rhythmic trapping, below). Alternatively, if it belonged to the present bivalve community, it may possibly have occupied a high level, epi-byssate position.

The presence of protobranchs indicates a high organic content in the original substrate. Extant Lucinacea generally live in environments where the food supply is so low that all available food particles must be accepted (Allen 1958, p. 480). This is achieved by their specialized sorting mechanism with the help of symbiotic bacteria. The suggestion of similar conditions at this locality at the time of sedimentation seems reasonable. The assumed low oxygen and high sulphur content of the substrate at Grogarnshuvud 1 might explain the low bivalve diversity with only two additional infaunal bivalve species, the deepest one, *Janeia silurica*, also assumed to have had symbiotic sulphur reducing bacteria (by analogy with its living relatives). *Ilionia prisca* most probably had a specially developed sorting mechanism as well as a strong adductor muscle, capable of powerful retraction and closure of the valves for efficiently discharging indigestible particles posteriorly. Its deep life position suggests that it lived in the oxygen-poor, sulphur-rich zone of the sediment, which strengthens the idea of a symbiosis with anaerobic bacteria. Other lucinid-solemyid associations have also been connected with fine-grained and poor-food habitats, e.g. the Cenozoic *Thyasira–Lucinoma–Solemya* association (Hickman, 1984).

Feeding capacity is one of the most important features upon which selection pressure acts in animal species (Stanley 1970, p. 79), and it appears that the unique feeding strategy of *Ilionia prisca* (a deep life position with an inferred anterior inhalant tube and a posterior exhalant system in combination with symbiosis with sulphur-oxidizing bacteria), seems to have been an optimal adaptation to an environment hostile to all other infaunal suspension feeding bivalves.
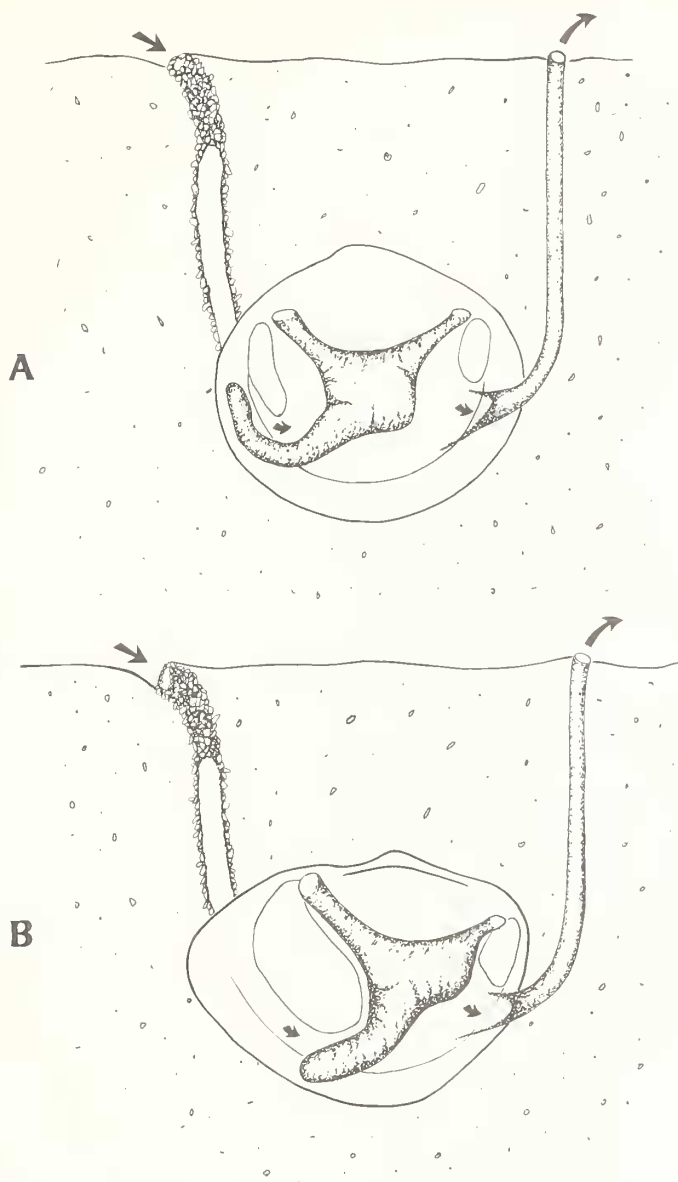
TEXT-FIG. 6. A, life position of Recent lucinacean bivalves (modified after Allen 1958; McAlester 1965); the foot, the sites of the adductor muscles (stippled) and the posterior exhalant siphon are shown. B, suggested life position and reconstruction of the foot and posterior exhalant siphon of *Ilionia prisca* (muscular impressions stippled); water is inhaled through a mucus lined tube; arrows indicate direction of water flow.

Preferred orientation

Grogarnshuvud 1 includes a series of beds of interlayered fine grained limestones and calcareous shales belonging to the Hemse Beds, units *c* and *d* (for detailed descriptions see Sundquist 1982).

At several horizons a large number of *in situ* specimens of *Ilionia prisca* can be observed contrasting conspicuously with the recently eroded bedding planes. In four of the beds abounding in *Ilionia prisca* (Nos 1, 2, 10, 11) the orientation of the bivalves was measured. In three of these
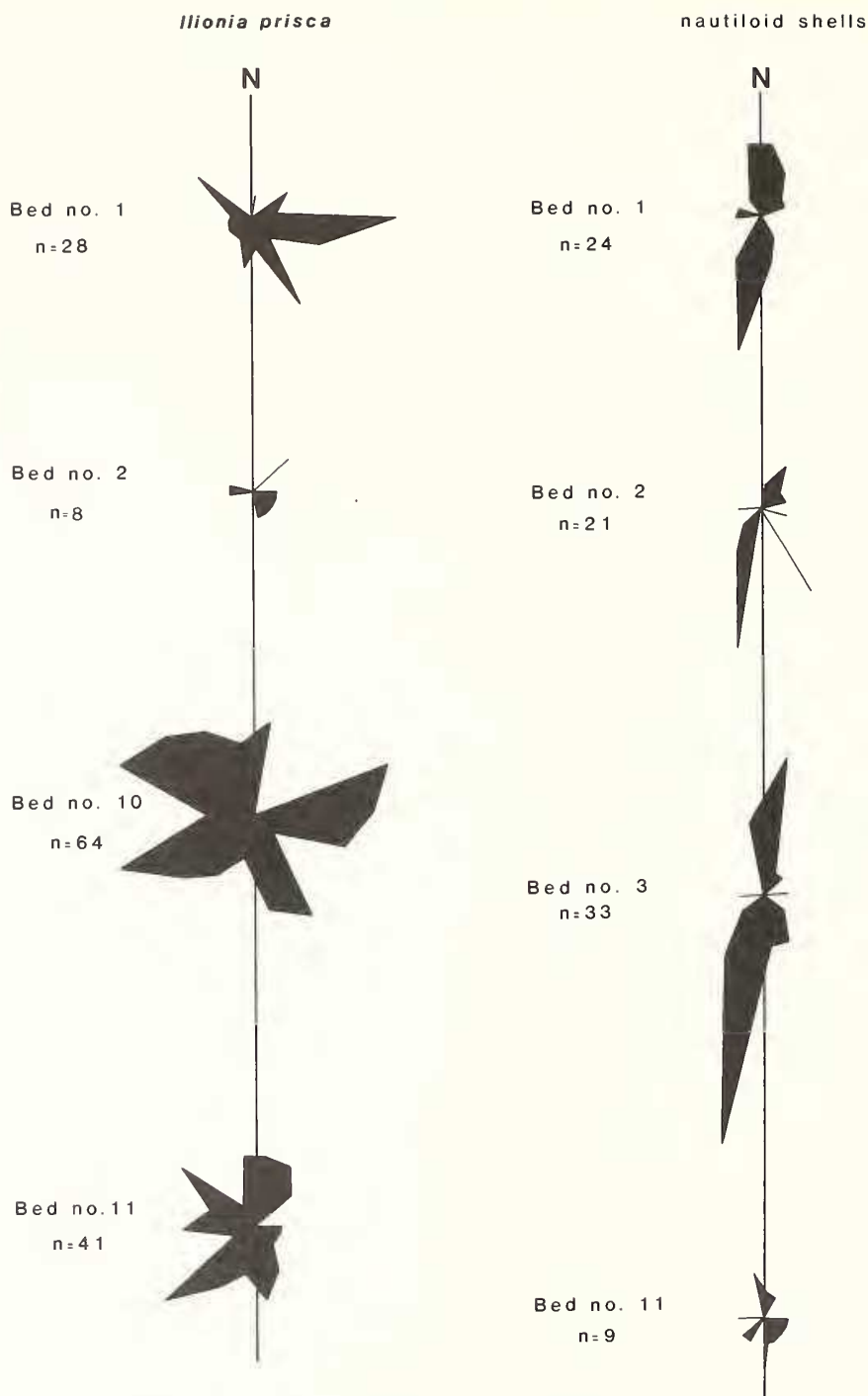
TEXT-FIG. 7. Rose diagram of direction of anterior end showing orientation of anteroposterior axis of *in situ* specimens of *Ilionia prisca* and of orthocone nautiloid shells on bedding planes at Grogarnshuvud 1. n = numbers of specimens.

beds (Nos 1, 2, 11) and an additional bed (No. 3 with less abundant *Ilionia prisca*) the orientation of orthoconic nautiloid shells was recorded. The results are presented in Text-figure 7.

Sundquist (1982, p. 85, fig. 4) made a similar study of nautiloid shell orientation in this locality. Bed No. 1 probably corresponds to Sundquist's No. 4, bed No. 2 to his No. 3, and bed No. 3 to his No. 2. Bed No. 10 lacks nautiloid shells while in bed 11 there are only eight recorded specimens.

In addition to the bivalve specimens *in situ* on the bedding planes a number of *in situ* specimens were found well within the limestone beds.

In principle the bivalves exhibit a quadro-polar, preferred *in situ* orientation with their anterior end pointed in approximately NW, SE, ENE, WSW directions, which seem to be consistent throughout the beds at this locality (Text-fig. 7). In bed No. 1 there is a dominant direction to the E, in bed No. 2 a dominant direction to the SE, whereas bed No. 11 lacks a dominant anterior direction to the SE.

Discussion. Some bivalves have evolved the behaviourial strategy of orienting themselves in a direction favourable for feeding. A few commensal species of Erycinacea, for example, orient themselves with their anterior end (where the inhalant siphon is situated) towards their host, due to chemokinetic response (Morton 1962). Other species of the same family are able to orient themselves with their anterior end to stimuli of light, gravity and lateral contact (Morton 1960). Some burrowing bivalves orient themselves preferentially with their posterior siphon against the prevailing current direction. For example, the alignment of *Anadara trapezia* is correlated with the direction and strength of tidal or wind-driven water currents (O'Gower and Nicol 1971). It is assumed that correct orientation of this bivalve would assist respiration, feeding and sanitation, and would possibly also lessen the chances of accidental dislodgement (O'Gower and Nicol 1971, p. 277). Some fresh-water bivalves also show preferred orientation in relation to water currents (J. Kříž, pers. comm. 1988).

As far as the orientation of *Ilionia prisca* is concerned, it may be related directly to the alignment of the orthocone nautiloid shells on the same bedding planes or to a factor which affected both the bivalves and the empty cephalopod shells. Sundquist (1982) concluded that the bipolar apex orientation of the nautiloid shells indicates a preferred orientation caused by wave action. The orientation pattern does not, however, form two completely opposing maxima, and is interpreted as the result of interacting forces of waves and wave currents. The wave progression is suggested to have been from ESE (Sundquist 1982, p. 85).

The orientation of the nautiloid shells in this paper (Text-fig. 7), agrees with those in Sundquist's study, thus strengthens the assumption of a fairly constant main wave progression from the ESE in this area at the time of sedimentation.

Assuming that the different beds at this locality were deposited under fairly constant conditions (Sundquist 1982, p. 86), the stable uniform orientation of the nautiloid shells may be taken as a criterion of a constant shore line direction, parallel to the anterior-posterior axis of the shells. Although caution should be taken in interpretations of palaeogeography based on locally restricted material, the shore line at this locality, as indicated by the elongated shells of nautiloids and gastropods, at the time of sedimentation seems to have been aligned roughly NNE–SSW. This direction agrees fairly well with earlier reconstructions of shore lines and palaeobathymetry on Gotland (Hadding 1958, Manten 1971, Laufeld 1974, Eriksson and Laufeld 1978, Bergman 1979, Sundquist 1982).

The orientation of the length axis of the bivalves of each individual bed at this locality is fairly constant, which is also the case with the nautiloid shells, indicating a wave progression direction from the ESE. Thus, it seems as though *Ilionia prisca* oriented itself with its anterior-posterior axis oblique to the prevailing wave direction, in which the suspended (food) particles travel. If so, its anterior inhalant mucus tube was facing the net transport of food particles (Text-fig. 8B; cf. similar life position of *Thyasira* and *Lucinoma* with the opening of their anterior mucus tube facing the current at the sediment/water interface, in Hickman 1984, fig. 9). Probably this orientation was more advantageous than if the bivalves were aligned in the same direction as water movement (Text-
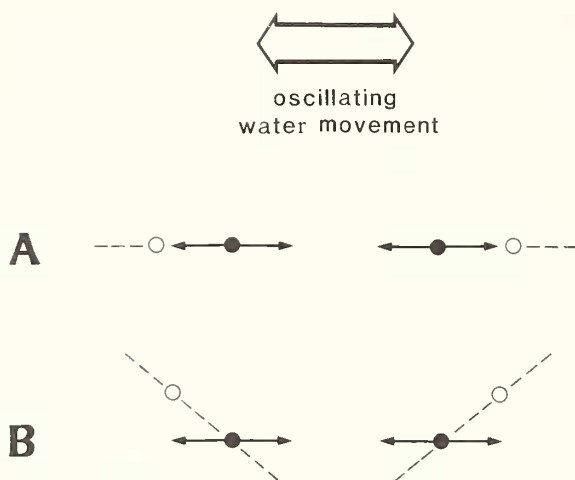
TEXT-FIG. 8. Orientation of anteroposterior axis (broken lines) of *Ilionia prisca* in relation to water movement. Anterior inhalant tube (open circle) and posterior exhalant siphon (filled circle), thin arrows showing direction of waste products. A, hypothetical in line-orientation. B, observed oblique orientation.

fig. 8A). In the latter case, with an oscillating wave movement, the chances of inhaling its own waste products are greater than in case of oblique orientation.

Rhythmic trapping

A number of the limestone beds at Grogarnshuvud 1 abound in *Ilionia prisca* while others contain few or no specimens. Each of the beds discussed is intercalated with calcareous shales. The thickness of the limestone beds ranges from 70 to 130 mm. The shales are usually 10 mm thick but can in places reach 60 mm (see also Sundquist 1982).

It is suggested that each limestone bed represents one life association of *Ilionia prisca*, although there is a conspicuous lack of juvenile specimens (Liljedahl, in prep.).

Sundquist (1982, pp. 87–89) assumes that the calcareous shale beds represents the final stage of a previous ephemeral incident, such as a storm, etc. The shales were deposited rhythmically and possibly some of them represent volcanic ash-falls rich in silica, indicated by the presence of silicified fossils. On such occasions a large number of floating nautiloid shells were stranded and oriented parallel to the shore due to storm-wave action. The water was heavily loaded with suspended particles, which eventually came to rest, resulting in a deposit considerably thicker than the present thin shale beds. The fouling of the water and/or sedimentation of the fine grained material most probably was catastrophic for the bivalves and the infaunal species were forced to escape.

However, when overburden stress reaches a critically high value, burrowing infaunal organisms can not escape burial. Experiments on living polychaete/bivalve communities show that this value (40 Kpa) corresponds to a burial depth of *c*. 28 cm (Nicols *et al.* 1978). Specimens of *Ilionia prisca* are found down to a depth of 10 cm or more in the sediment and with an overburden of a thick layer of clay (now considerably compacted). This limit could have been reached in the present community at Grogarnshuvud 1 and the infaunal bivalves fatally trapped. It seems as if no reworkers, including protobranch bivalves, gastropods, annelid worms etc. survived, since *Ilionia prisca* was preserved undisturbed in 'life' position.

As stated, specimens of *Ilionia prisca* have been found at different depths in the beds and even at the sediment surface (all orientation-measured specimens). A number of individuals are inclined, with their antero-posterior axis dipping at an angle of 10–15° to the bedding plane (Text-fig. 9). This suggests that these individuals were killed during the rocking movement of burrowing, perhaps while attempting to escape. According to Stanley (1972) and Nicols *et al.* (1978), in a series of experiments, individual burrowing ability of each bivalve species resulted in differences in escape efficiency. Although no escape structures have been found in the different beds at Grogarnshuvud, the slurry-like nature of the sediment may account for their absence.

TEXT-FIG. 9. *In situ* specimens of *Ilionia prisca* on eroded bedding surfaces, Grogarnshuvud 1, Ludlovian Hemse Beds. A, articulated specimen preserved as internal mould of surrounding sediment, ×0.6. B, articulated specimen preserved as druse filled internal mould, ×0·7.

The specimens found on the bedding planes either: (1) succeeded in escaping burial; their gills were, however, eventually clogged due to the large amount of fine grained suspension in the very turbid water; or (2) they were killed in 'life' position, or rather 'death' position after having burrowed themselves downwards in the sediment and later isolated by erosion caused by the ephemeral violent event. The presence of some specimens, preserved as drusy filled cavities (Text-fig. 9B), supports this latter assumption. They indicate extremely rapid burial and enough compaction forces to prevent the ligament to open the valves after soft part corruption.

The absence of *Ilionia prisca* from some of the beds may result from the sedimentation of the fine grained material not being rapid enough for catastrophic burial. Alternatively the high turbidity event may have been too short for the bivalves to be suffocated. In either case the bivalves might have been able to escape and survive. It is also possible that the bivalves had not yet colonized the area after the previous catastrophic event.

It seems as if only one or a few age classes colonized the area after each previous mud sedimentation event. Presumably either these individuals were killed during the following catastrophic incident before they were able to reproduce, or the environment was simply unfavourable for their young offspring (see Rhoads and Young 1970).

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